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Native distribution characteristics rather than functional traits explain preadaptation of invasive species to high-UV-B environments

Maria Hock[1,2] | Rainer Hofmann[3] | Franz Essl[4] | Petr Pyšek[5,6] | Helge Bruelheide[2,7] | Alexandra Erfmeier[1,7]

[1]Institute for Ecosystem Research/Geobotany, Kiel University, Kiel, Germany

[2]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

[3]Faculty of Agriculture and Life Sciences, Lincoln University, Lincoln, New Zealand

[4]Department of Botany and Biodiversity Research, University Vienna, Vienna, Austria

[5]Institute of Botany, Department of Invasion Ecology, Czech Academy of Sciences, Průhonice, Czech Republic

[6]Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic

[7]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Correspondence
Maria Hock, Institute for Ecosystem Research/Geobotany, Kiel University, Olshausenstr. 75, 24118, Kiel, Germany.
Email: mhock@ecology.uni-kiel.de

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Abstract

Aim: Alien species successfully colonize new ranges if they encounter favourable environmental conditions there and possess traits that match new challenges. Climate-matching approaches comparing native and exotic ranges mostly consider temperature and precipitation niches of alien species, but have largely ignored UV-B radiation. UV-B fundamentally differs between hemispheres, with much higher levels at southern than at northern latitudes. Consequently, UV-B might act at the global scale and present a so far neglected filter that species need to overcome when invading high-UV-B environments.

Location: We performed two multi-species common garden experiments, conducted in the native European range (Germany) and the high-UV-B exotic range (New Zealand) to test for preadaptation to UV-B.

Methods: We used 25 herbaceous species from open habitats, which we exposed in each range to three UV radiation treatments: (a) natural sunlight, (b) exclusion of UV-B while allowing natural UV-A, and (c) exclusion of UV-B and UV-A. We additionally used plant traits (TRY), global distribution data (GBIF, GloNAF) and global UV-B satellite data (glUV) to determine species-specific characteristics as fostering agents of UV-B tolerance. The joint analysis of experimental and macroecological data allowed quantification of species plasticity and identification of beneficial species traits in high-UV-B environments.

Results: Our results showed an overall limiting effect of UV-B in both common gardens but the UV-stress response tended to be more pronounced in the invaded range. Across all species, we found little evidence for preadaptation by functional plant traits. In contrast, preadaptation to climatic conditions related to the species' native UV-B niche was of greater importance for plant performance in the presence of UV-B radiation.

Main conclusions: For predicting alien species' ability to expand into high-UV-B environments, macroclimatic niche characteristics of the species' native range might

be better predictors than functional traits and should be more considered in future projection models.

KEYWORDS

alien species, climatic preadaptation, common garden, functional preadaptation, Germany, multi-species experiment, New Zealand, plant traits, species distribution, UV-B radiation

1 | INTRODUCTION

Alien species reach novel habitats due to human-mediated transport and expand into new ranges with sometimes severe consequences for indigenous plant communities and ecosystems and/or the local economy (see Blackburn et al., 2011; Heger, Saul, & Trepl, 2013; Richardson et al., 2000). Gaining a deeper understanding of mechanisms underlying the colonization of alien species in novel ranges is a major aim of invasion science. Thus, one research focus still addresses invasiveness of species including the identification of traits and characteristics that might be beneficial during establishment and spread into new habitats. While beneficial traits might already exist prior to the introduction elsewhere (e.g. DeWalt, Denslow, & Hamrick, 2004; Dlugosch & Parker, 2007; Elst et al., 2016), they might also be the outcome of evolutionary changes during colonization in the novel environment (e.g. Maron, Vilà, Bommarco, Elmendorf, & Beardsley, 2004; Qing et al., 2011). Favourable traits and mechanisms existing prior to invasion that may convey high aptitude for a particular environmental factor in a new region could result from evolution in the native range either (a) randomly ("drift"), (b) for a different purpose ("exaptation," Gould & Vrba, 1982) or (c) in consequence of selection by this particular environmental factor in the home range ("adaptation"). All these processes together are addressed as "preadaptation" in the present study (Agosta & Klemens, 2008; Pearson, Ortega, Eren, & Hierro, 2018). In fact, one of the most fundamental theories explaining plant invasions initially suggested that species preadapted to colonize a broad range of habitats may be considered "general-purpose-genotypes" (Baker, 1974; Parker, Rodriguez, & Loik, 2003).

Although it has become apparent that species traits alone only partly explain invasion success (Pyšek et al., 2009, 2015; Pyšek & Richardson, 2007), traits associated with high reproductive capacity (e.g. high seed number and seed persistence, short generation time) and vigorous growth (e.g. high specific leaf area and photosynthetic rate) have been shown to increase the likelihood of successful invasions (e.g. Baker, 1974; van Kleunen, Weber, & Fischer, 2010; Moravcová, Pyšek, Jarošík, Havlíčková, & Zákravský, 2010; Moravcová, Pyšek, Jarošík, & Pergl, 2015; Pyšek & Richardson, 2007; Whitney & Gabler, 2008). In *Centaurea stoebe*, for instance, a higher ploidy level was associated with increased invasive potential, probably due to a broader tolerance of environmental conditions and greater potential to rapidly evolve in the invaded range (Henery et al., 2010; see also Te Beest et al., 2011). Furthermore, invasiveness of species might be also attributable to high phenotypic plasticity in response to changing environmental conditions (Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006; Ghalambor et al., 2007; Lamarque, Lortie, Porté, & Delzon, 2015), for example, plastic root-foraging due to alterations in nutrient availability (Keser et al., 2015). Accordingly, species might evolve a high phenotypic plasticity after the introduction to a novel range (e.g. Moroney, Rundel, & Sork, 2013) or benefit from preadaptation by exhibiting high phenotypic plasticity already during establishment (e.g. Lamarque et al., 2013).

Beside these intrinsic (functional) plant traits, Curnutt (2000) distinguishes "extrinsic traits" associated with niche space that might preadapt species to establish more easily and to become invasive. For instance, a large native range might imply climatic preadaptation to a wide range of broad-scale abiotic conditions (Kalusová et al., 2017; Pyšek et al., 2009, 2015). It has been shown that invasion success of alien species is positively correlated with the level of climate—or more broadly environmental—matching between native and exotic range (e.g. Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). So far, modelling of alien species distributions has been largely based on climatic variables such as precipitation and temperature (e.g. Ahmad, Khuroo, Hamid, Charles, & Rashid, 2019; Petitpierre et al., 2012; Sheppard, Burns, & Stanley, 2016). While UV-B radiation is another macroclimatic factor that significantly differs at large scales and is subject to human impact, it has been rarely considered a potentially selective environmental filter in plant invasions to date. Notably, some experimental studies already addressed the impact of UV-B radiation on germination or growth of selected invasive species (Beckmann, Hock, Bruelheide, & Erfmeier, 2012; Hock, Beckmann, Hofmann, Bruelheide, & Erfmeier, 2015; Hock, Hofmann, Müller, & Erfmeier, 2019; Qaderi, Yeung, & Reid, 2008; Wang, Ma, Zhang, Siemann, & Zou, 2016).

Northern and southern hemispheres fundamentally differ in overall annual and maximum UV-B levels, in particular, when considering UV-B intensities in temperate regions at comparable latitudes, for example Central Europe and New Zealand representing two major donor and recipient areas of naturalized alien species (Seckmeyer & McKenzie, 1992; Godar, 2007; van Kleunen et al., 2015; Pyšek et al., 2017). UV-B intensities are not simply dependent on latitude and elevation but are also determined by the shorter earth-to-sun distance during the southern hemisphere summer and the higher solar elevation angle yielding in up to twofold higher UV-B intensities in the southern hemisphere compared to the northern one (McKenzie, Aucamp, Bais, Björn, & Ilyas, 2007; McKenzie et al., 2011). Global UV-B differences are thus

a fundamental phenomenon affecting plant life but remain subject to change, as UV-B levels are also influenced by anthropogenic impact, for example tropospheric aerosol emission levels (Watanabe, Takemura, Sudo, Yokohata, & Kawase, 2012). In general, plants respond to elevated UV-B radiation with delayed reproduction, decreased productivity, altered plant architecture and leaf morphology, such as thicker leaves, changes of leaf shape, reduced stem length, increased branching and altered root:shoot ratios (Kataria, Jajoo, & Guruprasad, 2014; Llorens et al., 2015; Robson, Klem, Urban, & Jansen, 2015; Suchar & Robberecht, 2016). At the cellular level, the main targets of biologically effective, high-energy UV-B radiation are nucleic acids, Calvin cycle enzymes and photosystem II proteins, which may result in photosynthesis apparatus damage (Kataria et al., 2014). Even though detrimental UV-B effects on plants have been comprehensively studied at the autecological level, this factor has been largely neglected as a potentially selective force for plant invasions.

To assess the relevance of UV-B radiation for plant invasions in high-UV-B environments, the present study aims at revealing whether the species' response to UV-B is driven by plant traits, climatic preadaptation acquired in the species' native range and the UV-B history in the native range. This approach is based on the assumption that functional preadaptation by plant traits and/or climatic preadaptation associated with species distribution and/or native UV-B niche characteristics might be important for species during colonization of high-UV-B environments. To test for potential preadaptation, plant performance has to be compared in the native and exotic ranges (Schlaepfer, Glaettli, Fischer, & van Kleunen, 2010). Ideally, plant responses to UV-B radiation should be studied under natural radiation conditions characterized by a typical relation of photosynthetically active radiation (PAR), UV-A and UV-B (Kuhlmann & Müller, 2011). Closely associated with UV-B, in particular, UV-A radiation is known for its mitigating effect under abiotic stress conditions (e.g. high UV B, drought), as it induces protective responses of the photosynthetic apparatus and therefore increases physiological resilience (Escobar-Bravo, Klinkhamer, & Leiss, 2017; Štroch et al., 2015; Verdaguer, Jansen, Llorens, Morales, & Neugart, 2017). Furthermore, the differences in the level of UV radiation between native and exotic ranges allow disentangling the effect of UV radiation on plant growth and development in the context of the local environments (Hock et al., 2019).

In two common garden experiments, we studied the role of preadaptation to UV-B radiation on 25 herbaceous species from open habitats and eleven families, both in the native northern hemisphere (Central Europe) and the invaded southern hemisphere (New Zealand). We established an UV radiation gradient in both common gardens to directly test for plant responses to this abiotic factor. We tested for preadaptation to elevated UV-B levels and addressed the following hypotheses: (a) Functional preadaptation to UV-B is modulated by functional plant traits. (b) Native range (UV-B) characteristics serve as suitable proxies for climatic preadaptation to high-UV-B environments. (c) Plant responses to the applied UV treatments within both common gardens are additionally reflected in the differences between the experimental sites Germany and New Zealand due to the existing differences in natural UV-B intensity between hemispheres. To our knowledge, this is the first study addressing preadaptation of alien species to elevated UV-B levels via multi-species common garden experiments in the native and invaded range.

2 | METHODS

2.1 | Experimental data

We conducted two multi-species common garden experiments in the native European range (Germany) and in the invaded range (New Zealand). In Germany, the experiment took place at the Botanical Garden of Kiel University (EPSG:3857 coordinates: N54.34583°, E10.11632°) during the northern hemisphere summer season 2015 (July–October), whereas the New Zealand common garden was established at Lincoln University (EPSG:3857 coordinates: S43.64506°, E172.4620°) and ran during the southern hemisphere summer season 2014/2015 (December–March). Common garden experiments are especially suitable to control for phenotypic plasticity effects and to consequently assess genetic differentiation and local adaptation of genotypes within species in a common environment (Kawecki & Ebert, 2004; Villemereuil, Gaggiotti, Mouterde, & Till-Bottraud, 2016). In the present study, the northern and southern hemisphere common gardens furthermore allowed investigating the impact of the naturally diverging environmental factor UV-B radiation on genotypes in an otherwise standardized environment to determine the UV-B preadaptation of this genotype (see "home vs. away" in Kawecki & Ebert, 2004).

In total, 25 herbaceous plant species were included in each experiment (n = 751 individuals), all native to Europe and naturalized in New Zealand (Allan Herbarium , 2000; Howell & Sawyer, 2006). Since we were interested in the role of preadaptation acquired in the species' native range, only seed material from the native Northern hemisphere was used for all species, resulting in 377 plant individuals tested in the German common garden and 374 in the New Zealand common garden. Seeds were either obtained from commercial seed companies or botanical gardens in 2014, and under similar conditions grown in both common gardens (see Table 1 for species list and seed origin information). We especially ensured that all seeds derived from outdoor populations, as growth and reproduction under natural radiation is the basic requirement for adaptation to UV radiation. All individuals were germinated in the greenhouse under controlled conditions in seedling trays and transferred to pots (2 litre) about 6–8 weeks later. Subsequently, 10-week old plants were assigned to experimental treatments.

In both common gardens, the plants were exposed to three UV treatments, including (a) full exposure to ambient, that is, natural UV-A and UV-B radiation (+UV-A/+UV-B), (b) exclusion of UV-B while allowing natural UV-A (+UV-A/-UV-B), and (c) total exclusion of both UV-A and UV-B wavelengths (-UV-A/-UV-B). To apply these

TABLE 1 Species list, seed origin information and species-specific experimental duration in the New Zealand and German common garden experiments, respectively. All species are listed as "naturalized" in New Zealand (Allan Herbarium, 2000; Howell & Sawyer, 2006)

Species	Family	Experimental duration [d]		Source	Year of collection	Location
		NZ	DE			
Antirrhinum majus	Scrophulariaceae	75	72	Botanical Gardens of MLU, Halle	2014	Halle, Sachsen-Anhalt
Artemisia absinthium	Asteraceae	102	75	Botanical Gardens of MLU, Halle	2013	Halle, Sachsen-Anhalt
Aurinia saxatilis	Brassicaceae	104	74	Botanical Gardens of MLU, Halle	2013	Halle, Sachsen-Anhalt
Centranthus ruber	Valerianaceae	73	73	Botanical Gardens of MLU, Halle	2012	Halle, Sachsen-Anhalt
Cerinthe major	Boraginaceae	75	72	Saatgut-Vielfalt	2013	Unspecified[a]
Cichorium intybus	Asteraceae	103	72	Botanical Gardens of MLU, Halle	2013	Wormsleben, Sachsen-Anhalt
Dianthus barbatus	Caryophyllaceae	109	76	Botanical Gardens of MLU, Halle	2013	Halle, Sachsen-Anhalt
Diplotaxis muralis	Brassicaceae	73	75	Botanical Gardens of MLU, Halle	2012	Halle, Sachsen-Anhalt
Inula helenium	Asteraceae	107	71	Botanical Gardens of MLU, Halle	2013	Halle, Sachsen-Anhalt
Leontodon autumnalis	Asteraceae	77	73	Rieger-Hofmann® GmbH	2013	Unspecified[a]
Linaria purpurea	Scrophulariaceae	77	76	Botanical Gardens of MLU, Halle	2014	Friedeburg, Sachsen-Anhalt
Lobularia maritima	Brassicaceae	73	77	Saatgut-Vielfalt	2013	Unspecified[a]
Malva neglecta	Malvaceae	77	75	Botanical Gardens of MLU, Halle	2011	Luckau, Brandenburg
Origanum vulgare	Lamiaceae	78	77	Rieger-Hofmann® GmbH	2013	unspecified[a]
Potentilla recta	Rosaceae	103	72	Botanical Gardens of MLU, Halle	2014	Halle, Sachsen-Anhalt
Prunella laciniata	Lamiaceae	110	72	Botanical Gardens of MLU, Halle	2012	Halle, Sachsen-Anhalt
Prunella vulgaris	Lamiaceae	111	75	Botanical Gardens of MLU, Halle	2013	Halle, Sachsen-Anhalt
Silene dioica	Caryophyllaceae	75	71	Botanical Gardens of MLU, Halle	2012	Halle, Sachsen-Anhalt
Silene latifolia	Caryophyllaceae	74	74	Botanical Gardens of MLU, Halle	2013	Halle, Sachsen-Anhalt
Tanacetum parthenium	Asteraceae	106	75	Botanical Gardens of MLU, Halle	2013	Halle, Sachsen-Anhalt
Tragopogon porrifolius	Asteraceae	104	74	Botanical Gardens of MLU, Halle	2014	Friedeburg, Sachsen-Anhalt
Trifolium medium	Fabaceae	100	75	Rieger-Hofmann® GmbH	2013	Unspecified[a]
Trifolium pratense	Fabaceae	78	73	Botanical Gardens of MLU, Halle	2012	Halle, Sachsen-Anhalt
Trifolium repens	Fabaceae	79	74	Botanical Gardens of MLU, Halle	2012	Halle, Sachsen-Anhalt
Veronica serpyllifolia	Plantaginaceae	77	76	Botanical Gardens of MLU, Halle	2013	Leipzig, Sachsen

[a]Seeds purchased by the companies "Saatgut-Vielfalt" and "Rieger-Hofmann® GmbH" originate from outdoor propagation areas in Germany and trace back to regional genotypes from wild populations.

UV treatments to the plants we used 18 experimental units (see Figure S1.1), of which six were equipped with Acrylic (PLEXIGLAS® GS 2,458 clear, Evonik Industries AG), PETG (Polycasa® PETG clear B1, ThyssenKrupp Plastics) or Polycarbonate sheets (Makrolon® GP clear 099, ThyssenKrupp Plastics), respectively. At maximum, one individual of each species was randomly assigned to each experimental unit, resulting in 3–6 replicates per species and treatment. In each experimental unit, about 25 individuals were randomly placed in a grid of 5 × 6 possible pot positions within an area of 1.2 m × 1.5 m. To counteract undesired shading effects of neighbouring plants, we randomly rearranged all individuals within the experimental units every other week. As the experimental units provided full shielding from precipitation, all plants were regularly watered during the experiments.

Plant height and maximum horizontal plant expansion, leaf number, maximum leaf width and maximum leaf length were monitored prior to the start of the experiment and, thereafter, on a monthly basis and at the harvest date. All individuals were harvested species-wise depending on the species-specific developmental climax, that is, the life-cycle stage of maximum biomass production. Therefore, the species were grown in the common gardens for different periods of time ranging from 73 to 77 days in the German experiment and from 73 to 107 days in the New Zealand experiment (see Table 1). During harvest, aboveground biomass and belowground biomass were separated and dried at 80°C for 48 hr. For each individual, leaf area, specific leaf area (SLA) and leaf dry matter content (LDMC) were determined as leaf functional traits. Depending on the species-specific sizes of the plants, several healthy and fully developed leaves were sampled per individual and traits were quantified based on leaf area, fresh weight and dry weight. These variables were experimentally determined for all 751 individuals in both common garden experiments in response to the different UV environments and served as response variables in the statistical analysis, hereafter indicated by the subscript "ind". Belowground biomass was determined for all

individuals in the German common garden, but only for 250 individuals in the New Zealand common garden, and thus, not further analysed as response variable.

To characterize climatic conditions at both experimental sites, we used official climate data for Germany from the Climate Data Center of the Deutscher Wetterdienst (DWD, http://www.dwd.de/EN/climate_environment/cdc/cdc.html) and the Federal Office for Radiation Protection (BfS, www.bfs.de). New Zealand climate data were obtained from the National Climate Database (NIWA, https://cliflo.niwa.co.nz/) and the UV Atlas (Version 2.2). During their respective runtimes, both experiments had similar temperature conditions with a maximum temperature of about 30°C but a slightly lower minimum temperature in New Zealand (DE: 4.1–4.7°C, NZ: 2.1°C). Depending on the species-specific experimental runtime, plants experienced in total up to 495 sunshine hours in Germany and 760 hr of sun in New Zealand, resulting on average in one more sunshine hour per experimental day in New Zealand. The mean daily global radiation dose was about twice as high in the New Zealand experiment compared to the native range common garden. UV-B intensities showed a significant difference between both sites with about 2.5 times higher daily UV-B dose in the New Zealand experiment and, consequently, a maximum UV-B radiation sum of 974 kJ/m^2 in Germany compared to 3,454 kJ/m^2. All climate data information with specification of data source and respective measuring stations is listed in supplementary Table S2.1.

2.2 | Species' trait data—functional preadaptation

As plant species traits with the potential to indicate functional preadaptation to UV radiation, we chose plant height, seed dry weight and several functional leaf traits (leaf area, leaf persistence, leaf shape, specific leaf area (SLA), leaf dry matter content (LDMC)). Especially, leaf traits are considered to be strongly responsive to UV-B and are therefore assumed to play a major role in photoprotection abilities of plants (Chen et al., 2013; Robson & Aphalo, 2012;

TABLE 2 Preadaptation indicators: Species traits and biogeographic (i.e. native and exotic range) characteristics used to test for functional preadaptation and for climatic preadaptation, respectively. Range refers to the raw data range describing the diversity of the investigated species pool

Predictor	Description/calculation	Source of information	Range
Species traits			
SLA_{spec} [m^2/kg]	Specific leaf area (leaf area/leaf dry weight)	Experimental data	7.75–30.74
$LDMC_{spec}$ [%]	Leaf dry matter content (leaf dry weight/ leaf fresh weight)	Experimental data	12.96–34.08
Leaf area [cm^2]		Experimental data	0.59–116.46
Leaf shape	2 levels: simple versus pinnate/small	Personal observation	factorial
Leaf persistence	2 levels: persistent versus short-lived (during summer or over-wintering)	TRY database [1 - 6]	factorial
Seed dry weight [mg]		TRY database [1 - 19]	0.05–50.40
$Plant\ height_{spec}$ [cm]		Experimental data	8.67–55.17
Biogeographic characteristics			
Native range size [grid cells]	Number of native glUV grid cells	GRIN/KEW native range information	13–4916
Exotic range size [regions]	Number of exotic GloNAF regions	GloNAF information	2–211
Expansion index	= exotic range size/ native range size based on respective glUV grid cell numbers	GRIN/KEW native range information, GloNAF information	0.005–83.563
Native UV-B niche maximum [J m^{-2} day^{-1}]	Native range maximum of mean UV-B of the highest month	glUV (UVB3)	5457–10221
Native UV-B niche mean [J m^{-2} day^{-1}]	Native range mean of sum of monthly mean UV-B during highest quarter (summer)	glUV (UVB5)	8804–14763
Native UV-B niche width [J m^{-2} day^{-1}]	= native range maximum sum of monthly mean UV-B during highest quarter (summer) - native range minimum sum of monthly mean UV-B during highest quarter (summer)	glUV (UVB5)	2098–25053
UV-B novelty index	= exotic range annual mean UV-B/ native range annual mean UV-B	glUV (UVB1)	0.57–1.44

Note: TRY data set references: [1]Kühn, Durka, and Klotz (2004), [2]Kleyer et al. (2008), [3]Campetella et al. (2011), [4]Gachet, Véla, and Tatoni (2005), [5]Green (2009), [6]Royal Botanical Gardens KEW (2008), [7]Wright et al. (2004), [8]Fitter and Peat (1994), [9]Kirkup, Malcolm, Christian, and Paton (2005), [10]Meziane and Shipley (1999), [11]Dainese and Bragazza (2012), [12]Hickler (1999), [13]Garnier et al. (2007), [14]Everwand, Fry, Eggers, and Manning (2014), [15]Hill, Preston, and Roy (2004), [16]Fry, Power, and Manning (2014), [17]Shipley and Vu (2002), [18]Kattge, Knorr, Raddatz, and Wirth (2009), and [19]Reich, Oleksyn, and Wright (2009).

Václavík, Beckmann, Cord, & Bindewald, 2017). Plant height and seed dry weight were further included, as they correlate with plant fitness and reproduction strategies, but also differ among life forms (He, Zhang, & Dong, 2004). To characterize each of the 25 species included in the experimental species pool of both common garden experiments, we used a subset of some experimental response variables from the native common garden experiment to calculate species-specific mean trait values, hereafter indicated by the subscript "spec." In general, we considered the full UV exclusion treatment in the native common garden as a reference to derive baseline information on species-specific traits. We thus calculated plant height$_{spec}$, leaf area, SLA$_{spec}$ and LDMC$_{spec}$ from the experimental performance data as species-specific trait mean of all individuals in the German experiment under full UV exclusion conditions. Additionally, seed dry weight and leaf persistence data of all 25 species were obtained from the Plant Trait Database TRY (Kattge et al., 2011). Leaf shape was identified and assigned to categories by visual inspection. Thus, for all eight species traits 25 species-specific values were derived from different sources and served as predictors in the statistical analysis. Information about all traits used in the analyses and the respective data source is summarized in Table 2.

2.3 | Biogeographic characteristics—climatic preadaptation

We defined biogeographic characteristics for our study species, to depict species' native distribution patterns and the resulting native UV-B niche as proxies for a general preadaptation to a broad range of abiotic conditions or even direct UV-B preadaptation. For all study species, occurrence data were requested from the Global Biodiversity Information Facility database (GBIF, available from: https://www.gbif.org/, see Table S3.2 for list of obtained data sets) in June 2017 via R (Version 3.5.3, R Core Team, 2019) using the function "occ_search" (package "rgbif," Chamberlain et al., 2019; Chamberlain & Boettinger, 2017) to obtain all occurrences with latitude/longitude reference ("hasCoordinate = TRUE") and without spatial issues ("hasGeospatialIssue = FALSE"). The Global Naturalized Alien Flora (GloNAF, https://glonaf.org/) provided information about the naturalized range of all study species based their distribution in 843 GloNAF regions; only species reported as naturalized in the invaded range (following the definition of Blackburn et al., 2011; Richardson et al., 2000) are included in the database (van Kleunen et al., 2015, 2019; Pyšek et al., 2017). Additional information about the native range was obtained from the Germplasm Resource Information Network (GRIN, https://www.grin-global.org/) and Kew World Checklist (http://apps.kew.org/wcsp/home.do) based on the World Geographical Scheme for Recording Plant Distributions developed by the international Biodiversity Information Standards (TDWG, http://www.tdwg.org/). Subsequently, we merged species distribution data with TDWG/GloNAF information by a spatial overlay of shapefiles using the function "over" in R (package "sp," Bivand, Pebesma, & Gomez-Rubio, 2013; Pebesma & Bivand, 2005) to assign status information (native, exotic) to each GBIF species occurrence. Occurrence-specific information on UV-B characteristics was added by

TABLE 3 Significance table of model selection analysis—significance levels ($p < .001$ ***, $p < .01$ **, $p < .05$ *) are given for effects of the experimental main factors Exp = experimental site (DE versus. NZ), UV = UV treatment (+UV-A|+UV-B versus. +UV-A|-UV-B versus. –UV-A|-UV-B), their interaction, exp. dur. = experimental duration, the biogeographic characteristics in interaction with "Exp" and "UV," and the (functional) plant traits in interaction with "Exp" and "UV" on the experimental response variables. Terms dropped during model selection are marked in dark grey, and all remaining terms of the final model are marked in light grey

	Exp. predictors				Climatic preadaptation indicators/ interactions													
					Nat. range		Ex. range		Expansion		UVB max			UVB mean		UVB width		
Experimental response	Exp	UV	Exp:UV	exp. dur.		Exp		UV		Exp		UV		Exp	UV		Exp	UV
Abovegr. biomass		**					*	*										**
Plant height$_{ind}$				***		*												
Max. expansion		***		**		***						*			***			*
Leaf number	***			***	**			***				**			*		***	**
Max. leaf length	***	*									**				*			
Max. leaf width	*	*																
SLA$_{ind}$	***	*						***		***			***					***
LDMC$_{ind}$	*	*						**		*			**			*		***

Note: Climatic and functional "preadaptation indicators": Nat. range = native range size, Ex. range = exotic range size, Expansion = expansion index, UVB max = native UV-B niche maximum, UVB mean = native UV-B niche mean, UVB width = native UV-B niche width, Novelty = UV-B novelty index, SLA$_{spec}$ = specific leaf area, LDMC$_{spec}$ = leaf dry matter content, Leaf persist = leaf persistence.

matching (function "extract," package "raster," Hijmans, 2019) species' occurrence data with global UV-B satellite data with a spatial resolution of 15 arc-minutes (glUV, Beckmann et al., 2014).

From the merged occurrence data, we calculated the following biogeographic characteristics of exotic and native range that are supposed to be indicative for climatic preadaptation: native range size, exotic range size, native UV-B niche maximum, native UV-B niche mean, and native UV-B niche width (Table 2). We calculated two indices: (a) "Expansion index" describes the exotic range size in relation to the native range size as an indicator for species' ability to spread extensively beyond their native range. (b) "UV-B novelty index" indicates whether, and to what degree, UV-B intensity level in the exotic range is higher than in the native range and consequently represents a novel environmental factor. The "UV-B novelty index" is calculated as the ratio of the exotic range annual mean UV-B and the native range annual mean UV-B (for detailed description of indices see Table 2).

2.4 | Statistical analysis

As we were not interested in species-specific differences, but overall effects across the entire species pool, we standardized all experimental response variables within species by *z*-transformation and analysed the resulting *z*-scores. The standardization of absolute changes in response variables (raw scores) results in a comparable expression of the within-species response to different environments as number of species-specific standard deviations (*z*-scores) and thus accounts for absolute species-inherent differences. Thus, we jointly analysed the experimental plant responses of all 751 individuals of 25 different species from both common garden experiments in Germany and New Zealand. While the experimental data derived at the individual level (subscript "ind") served as response variables, species distribution data and functional trait data obtained at the species level (subscript "spec") were considered as species-specific traits that potentially promote alien species spread to high-UV-B environments and thus may be considered as "preadaptation indicators." These "preadaptation indicators" could either be plant (functional) traits or biogeographic characteristics associated with species distribution patterns and the respective native UV-B niche (Table 2).

To identify preadaptation, we tested for significant effects of "preadaptation indicators" on experimental response variables in different UV environments. For best models identification, the "step" function (package: "lmerTest") was applied to linear mixed models (function "lmer," package: "lmerTest") in R (Version 3.5.3, R Core Team, 2019). "Step" performs automatic backward elimination of effects of linear mixed effect models one at a time. Elimination of the fixed part is done by the principle of marginality, that is, the highest order interactions are tested first and if significant, the lower order effects are not tested for significance (according to "lmerTest" package description, Kuznetsova, Brockhoff, & Christensen, 2017).

Prior to model selection, we set up the "full models" to explain our experimental plant response in different UV-B environments: We used the z-scores of our experimental data from both common gardens as response variables to test for effects of "experimental

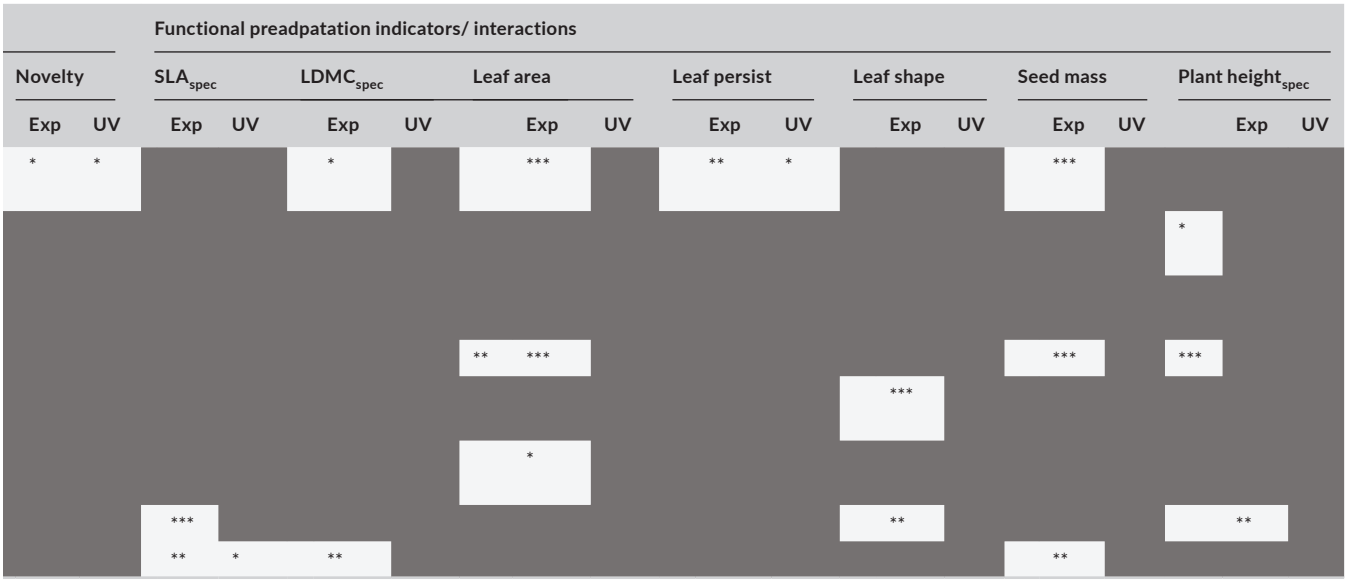

TABLE 4 Fixed-effect results of final mixed-model analysis. Degrees of freedom (df_N = numerator, df_D = denominator), *F*-statistics (*F*) and significance values (*p*) are provided for all remaining predictors after model selection. For random effect results, see Table S5.4

Aboveground biomass					*Plant height*					*Max. plant expansion*					*Leaf number*				
Predictor	df_N	df_D	*F*	*p*	**Predictor**	df_N	df_D	*F*	*p*	**Predictor**	df_N	df_D	*F*	*p*	**Predictor**	df_N	df_D	*F*	*p*
Exp	1	33.5	1.272	.268	Exp	1	43.6	0.343	.561	Exp	1	42.4	1.624	.210	Exp	1	34.7	15.239	<.001***
UV	2	672.3	5.871	.003**	UV	2	692.6	0.703	.495	UV	2	682.9	8.137	<.001***	UV	2	31.9	1.676	.203
Exp: UV	2	103.8	1.447	.240	Exp: UV	2	692.6	0.684	.505	Exp: UV	2	85.7	0.074	.929	Exp: UV	2	107.8	0.717	.490
exp. duration	1	30.7	1.012	.322	exp. duration	1	41.6	20.437	<.001***	exp. duration	1	41.3	7.824	.008**	exp. duration	1	30.9	28.859	<.001***
Ex. range	1	31.4	0.015	.903	Nat. range	1	43.0	0.678	.415	Nat. range	1	46.0	3.083	.086	Ex. range	1	33.0	0.682	.415
Ex. range: Exp	1	30.2	6.985	.013*	Nat. range: Exp	1	43.4	4.950	.031*	Nat. range: Exp	1	41.2	24.401	<.001***	Ex. range: Exp	1	33.5	24.829	<.001***
LDMC	1	31.7	0.001	.980	Plant height	1	39.7	5.829	.020*	UVB max	1	41.7	1.098	.301	Leaf area	1	29.9	9.576	.004**
LDMC: Exp	1	30.6	6.476	.016*						UVB max: Exp	1	42.6	5.356	.026*	Leaf area: Exp	1	28.4	51.704	<.001***
Leaf area	1	29.3	1.101	.303						UVB mean	1	40.2	0.014	.908	Nat. range	1	38.0	8.088	.007**
Leaf area: Exp	1	31.6	21.258	<.001***						UVB mean: UV	2	667.4	7.416	<.001***	Plant height	1	32.7	20.931	<.001***
Leaf persist.	1	29.6	0.824	.372						UVB width	1	42.9	1.567	.217	Seed mass	1	30.2	2.937	.097
Leaf persist.: Exp	1	30.8	8.376	.007**						UVB width: UV	2	673.8	3.666	.026*	Seed mass: Exp	1	36.4	28.930	<.001***
Leaf persist.: UV	2	669.0	4.167	.016*											UVB max	1	38.7	12.600	.001**
Nat. range	1	33.7	2.979	.094											UVB mean	1	34.7	5.835	.021*
Nat. range: UV	2	671.7	3.842	.022*											UVB width	1	39.8	14.034	<.001***
Novelty	1	28.5	0.063	.804											UVB width: Exp	1	36.0	11.317	.002**
Novelty: Exp	1	31.0	4.375	.045*															
Novelty: UV	2	668.5	3.990	.019*															
Seed mass	1	29.2	0.207	.653															
Seed mass: Exp	1	28.5	20.314	<.001***															
UVB max	1	31.3	0.501	.484															
UVB max: UV	2	670.1	4.772	.009**															
UVB width	1	32.1	1.186	.284															
UVB width: UV	2	671.8	5.172	.006**															

(Continues)

TABLE 4 (Continued)

Max. leaf length					Max. leaf width					Specific leaf area					Leaf dry matter content				
Predictor	df_N	df_D	***F***	***p***	**Predictor**	df_N	df_D	***F***	***p***	**Predictor**	df_N	df_D	***F***	***p***	**Predictor**	df_N	df_D	***F***	***p***
Exp	1	43.2	38.532	<.001***	Exp	1	45.7	4.753	.034*	Exp	1	24.0	22.412	<.001***	Exp	1	23.6	5.159	.033*
UV	2	683.6	3.619	.027*	UV	2	22.9	3.576	.045*	UV	2	24.3	4.819	.017*	UV	2	666.7	4.486	.012*
Exp: UV	2	24.1	1.150	.334	Exp: UV	2	29.6	1.645	.210	Exp: UV	2	90.6	0.137	.873	Exp: UV	2	20.4	0.190	.828
exp. duration	1	39.3	2.254	.141	exp. duration	1	39.2	0.344	.561	exp. duration	1	27.9	0.128	.723	exp. duration	1	23.6	1.759	.197
Expansion	1	35.1	0.073	.789	Leaf area	1	39.1	0.023	.880	Ex. range	1	28.8	0.012	.915	Ex. range	1	27.3	0.671	.420
Expansion: UV	2	659.7	4.891	.008**	Leaf area: Exp	1	41.4	5.692	.022*	Ex. range: Exp	1	30.0	18.851	<.001***	Ex. range: Exp	1	27.7	9.050	.006**
Leaf shape	1	40.9	0.015	.904						Expansion	1	23.4	0.539	.470	Expansion	1	22.2	0.024	.879
Leaf shape: Exp	1	41.3	19.894	<.001***						Expansion: Exp	1	24.1	29.735	<.001***	Expansion: Exp	1	21.9	7.899	.010*
UVB mean	1	37.1	0.088	.768						Leaf shape	1	25.4	1.631	.213	LDMC	1	26.1	1.007	.325
UVB mean: UV	2	1.0	3.199	.041*						Leaf shape: Exp	1	26.1	9.105	.006**	LDMC: Exp	1	25.4	9.295	.005**
										Plant height	1	25.6	0.107	.746	Seed mass	1	23.1	0.086	.772
										Plant height: Exp	1	26.6	13.529	.001**	Seed mass: Exp	1	22.4	13.530	.001**
										SLA	1	23.1	0.356	.556	SLA	1	23.7	0.171	.683
										SLA: Exp	1	23.4	25.732	<.001***	SLA: Exp	1	23.8	10.835	.003**
										UVB max	1	28.4	0.510	.481	SLA: UV	2	647.0	0.780	.022*
										UVB max: Exp	1	29.3	22.625	<.001***	UVB max	1	25.9	10.509	.385
										UVB mean	1	28.0	0.581	.452	UVB max: Exp	1	23.8	0.213	.004**
										UVB mean: Exp	1	28.9	14.127	<.001***	UVB mean	1	25.4	0.213	.648
										UVB width	1	28.1	0.623	.437	UVB mean: UV	2	647.5	4.397	.013*
										UVB width: Exp	1	29.0	26.088	<.001***	UVB width	1	25.8	0.740	.398
															UVB width: Exp	1	24.1	16.252	<.001***

site" (DE, NZ), "UV treatment" (-UV-A|-UV-B, +UV-A|-UV-B, +UV-A|+UV-B) and all 14 "preadaptation indicators." We also included the interaction effect of "UV treatment" and "experimental site." For each "preadaptation indicator," also the interaction effects with "experimental site" and with "UV treatment," respectively, were considered to particularly test for the importance of species characteristics on plant performance in different UV environments displayed by either global UV intensity differences between Germany and New Zealand or the different UV treatments applied within the experimental sites. Consequently, the "full model" contained 45 fixed (interaction) effects and we additionally included "day of harvest" as covariate to consider species-specific differences in experimental duration. Furthermore, we defined five nested random effects to correct for the block effect of UV treatment units ("unit") and for identity effects of species or family: "unit × experimental site," "unit × UV treatment," "species × experimental site," "species × UV treatment" and "family × species." We applied a model selection to the full model but strictly kept "experimental site," "UV treatment" and their interaction as well as "day of harvest" by definition in the final model. Interaction plots provide predicted values of z-scores obtained by the function "Effect" from package "effects" (Fox & Weisberg, 2019).

3 | RESULTS

3.1 | Effects of "UV treatment" and "experimental site" on plant performance

Aboveground biomass (p = .003) and maximum horizontal plant expansion (p < .001, see Tables 3 and 4) were significantly reduced by the presence of UV-A and/or UV-B radiation. We found a significantly reduced maximum leaf length (p = .027), maximum leaf width (p = .045) and specific leaf area$_{ind}$ (p = .017) under full solar radiation compared to the filter treatments in both experiments. In contrast, leaf dry matter content$_{ind}$ was highest in presence of UV-B radiation (p = .012). Plants in the New Zealand experiment produced more leaves (p < .001) than individuals in the German common garden. Maximum leaf length (p < .001) and width (p = .034), as well as specific leaf area$_{ind}$ (p < .001) were lower in the New Zealand experiment compared to the German common garden. Leaf dry matter content$_{ind}$ was significantly higher in the New Zealand common garden than in the German experiment (p = .033). We did not observe any significant interaction effects of "experimental site" and "UV treatment" among all response variables.

3.2 | Interaction effects of "preadaptation indicators" with "UV treatment" and "experimental site"

Regarding the study aim to identify suitable traits in the context of appropriate preadaptation to high-UV-B environments, corresponding interaction effects of preadaptation indicators with the experimental predictors "UV treatment" and "experimental site"—both representing different UV-B environments—are most interesting and will be described and discussed in the following.

3.2.1 | i) Species' traits—functional preadaptation

Leaf persistence displayed significant interaction effects with UV and the experimental site (see Tables 3 and 4): Species with persistent leaves showed higher aboveground biomass in the presence of UV-B radiation than species with short-lived leaves (p = .016, Figure 1a). A similar effect of leaf persistence on aboveground biomass was found in the New Zealand experiment compared to the German common garden (p = .007, Figure 1b). In the presence of UV-B radiation species with higher specific leaf area$_{spec}$ responded with a stronger increase in LDMC$_{ind}$, whereas at reduced levels of UV there was a negative relationship between SLA$_{spec}$ and LDMC$_{ind}$ (p = .022, Figure 1c). Those species also showed higher LDMC$_{ind}$ in the New Zealand experiment (p = .003, Figure 1d). All other plant traits showed no interaction effects with "UV treatment."

3.2.2 | ii) Biogeographic characteristics—climatic preadaptation

Six of the seven biogeographic characteristics showed significant interactions with "UV treatment" on the experimental response variables. Among them, especially the native UV-B niche mean turned out to be most important for three response variables. Across response variables, aboveground biomass was the most responsive to the biogeographic characteristics (Tables 3 and 4).

Species experiencing a much higher UV-B intensity in the exotic than in the native range (high "UV-B novelty index") showed a higher aboveground biomass in the UV-B exposure treatment (p = .019, Figure 2a) and, regardless of the UV treatments, were more productive in the New Zealand common garden than in the German one (p = .045, Figure 2b). Under UV-B radiation aboveground biomass showed a negative relationship with the species' native range UV-B niche width (p = .006), but a positive relationship with native range maximum UV-B of the highest month (p = .009). In the presence of UV-B radiation higher aboveground biomass was achieved by species with larger native range size (p = .022, Figure 2c). A strong positive relationship between the native UV-B niche mean and leaf dry matter content was observed in presence of UV-B (p = .013, Figure 2d). Higher native range mean UV-B intensity of the highest quarter (p < .001, Figure 3a) was significantly linked to an increase in maximum horizontal plant expansion in an UV-B environment. The general decrease of maximum horizontal plant expansion with native range UV-B niche width was lowest in presence of UV-B radiation (p = .026, Figure 3b). Compared to the full UV exposure

(+UV-A|+UV-B) and full UV exclusion (-UV-A|-UV-B), in the "UV-A only" treatment (+UVA|-UVB) maximum leaf length and native range mean UV-B intensity of the highest quarter showed a negative relationship (p = .041, Figure 3c). Leaves were significantly reduced in size in response to UV-B radiation with increasing "expansion index" of a species (p = .008, Figure 3d).

Furthermore, the statistical analysis revealed several other significant interactions of "preadaptation indicators" with "experimental site," which are not being discussed in the following. These interactions showed no evidence for a corresponding interaction effect of "preadaptation indicator" with "UV treatment" and, therefore, are likely to arise from UV-independent differences between Germany and New Zealand (see Tables 3 and 4).

4 | DISCUSSION

4.1 | Plant performance in different UV environments

The present study allows to assess the effects of UV radiation at two scales—within and between the two experimental sites—as the three UV treatments were applied in both experiments. The UV treatments significantly affected productivity, plant architecture and leaf traits, and allowed for the comparison of ambient solar radiation with two artificial UV environments to disentangle the ecologically inseparable effects of UV-A and UV-B. Most differences in plant responses occurred from presence/absence of UV-B radiation; however, a few significant "UV treatment" effects highlight the additional impact of UV-A radiation. The "UV-A only" treatment (+UV-A|-UV-B) mostly caused plant responses with absolute values between the "full solar radiation" level (+UV-A|+UV-B) and the "full UV exclosure" level (-UV-A|-UV-B). UV-A radiation is less detrimental for plant metabolism and has been even associated with a not fully understood mitigation effect in combination with UV-B in previous studies (Verdaguer et al., 2017).

Aboveground biomass, maximum horizontal plant expansion, maximum leaf length and leaf width were significantly lower in the presence of UV-B radiation, as previously shown in several studies (e.g. Bacelar, Moutinho-Pereira, Ferreira, & Correia, 2015; Hock et al., 2019; Robson et al., 2015; Suchar & Robberecht, 2014). Leaves exposed to full solar radiation were overall characterized by reduced specific leaf area but increased leaf dry matter content. Decreased UV-B sensitivity of smaller and thicker leaves has been repeatedly described for several plant species, due to UV-B shielding of the upper cell layers and a consequently better protected photosynthetic apparatus in the subjacent leaf tissue (e.g. Chen et al., 2016; Qaderi et al., 2008; Robson & Aphalo, 2012).

Higher leaf number of plants in the New Zealand experiment either indicates a generally more productive environment in comparison to the German common garden (see Hock et al., 2019) or a functional response to different environmental conditions that could not be controlled for in the experiments. Such differences might be a result of several biotic and abiotic factors, most notably those related to higher temperature or more sunshine hours, but might also derive from altered biotic interactions. However, in line with the effects of the UV treatments, individuals in the New Zealand experiment showed significantly reduced maximum leaf length, maximum leaf width and specific leaf $area_{ind}$, accompanied by higher leaf dry matter $content_{ind}$ very likely due to higher UV-B intensities in the southern hemisphere common garden. These results highlight the significance of prevailing differences in global UV intensity between native and exotic ranges of the plant species studied (Beckmann et al., 2012; Hock et al., 2019).

Although it is most notable that these effects were consistent across multiple species and regions with different overall UV radiation intensity, UV radiation appears to similarly affect plant performance in both common garden experiments, as we did not find any significant interaction effects of "UV treatment" and "experimental site." However, if the overall effect of UV-B radiation is similar by trend independent of the region but different in the intensity, it may hold that preadaptation to UV-B radiation can significantly pay-off for invasion success of species and help explaining the differences between successful colonization and invasion failure (see Gallien, Thornhill, Zurell, Miller, & Richardson, 2019). Admittedly, we cannot directly relate the experimentally determined plant performance under UV-B exposure to the invasive potential of the study species in high-UV-B environments (see Table S4.3). The artificial experimental settings in both common gardens do not display the complex interplay of biotic and abiotic factors under natural conditions. Nevertheless, UV-B preadaptation might be one important factor during species colonization of high-UV-B environments and, thus, may be worth to be additionally considered in future risk assessment.

4.2 | Evidence for functional preadaptation to high-UV-B environments

We found only little evidence for preadaptation at the functional plant trait level of the studied species to UV-B. Interestingly, leaf persistence and specific leaf $area_{spec}$ were important for plant responses to UV-B radiation and the respective effects indicate the fundamental role in the photoprotection measures of leaves. Our study revealed a general advantage of plant species with persistent leaves under UV-B exposure, whereas species with short-lived leaves experienced a pronounced aboveground biomass reduction under these conditions. This effect confirms preliminary findings of generally more efficient photoprotection in persistent leaves due to a higher investment in structures and mechanisms to avoid photodamage by high-energy UV radiation (Mason & Donovan, 2015; Wright et al., 2004). Higher leaf dry matter $content_{ind}$ in response to UV-B indicates denser multilayered leaf tissue with higher resilience to photodamage (Bacelar et al., 2015; Hock et al., 2019; Robson et al., 2015). At the global level, high irradiance environments are usually characterized by plants with

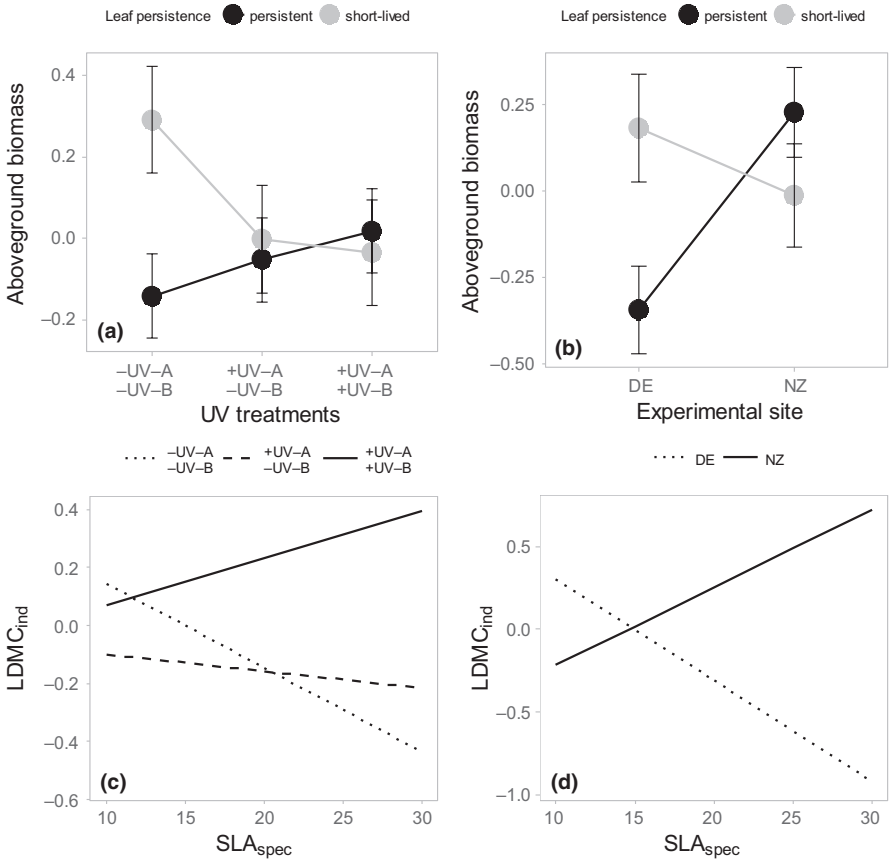

FIGURE 1 (a-d): Test for functional preadaptation: Reaction norms for aboveground biomass of species with persistent leaves (black) and species with short-lived leaves (grey) (a) across the different UV treatments and (b) across the experimental sites Germany (DE) and New Zealand (NZ); effects of species-specific specific leaf area (SLA_{spec}, [m^2/kg]) on leaf dry matter content ($LDMC_{ind}$) (c) across the different UV treatments and (d) across the experimental sites Germany (DE) and New Zealand (NZ). Predicted values of *z*-scores (± *SE*) from the respective full statistical model identified by model selection are shown for experimentally determined dependent variables

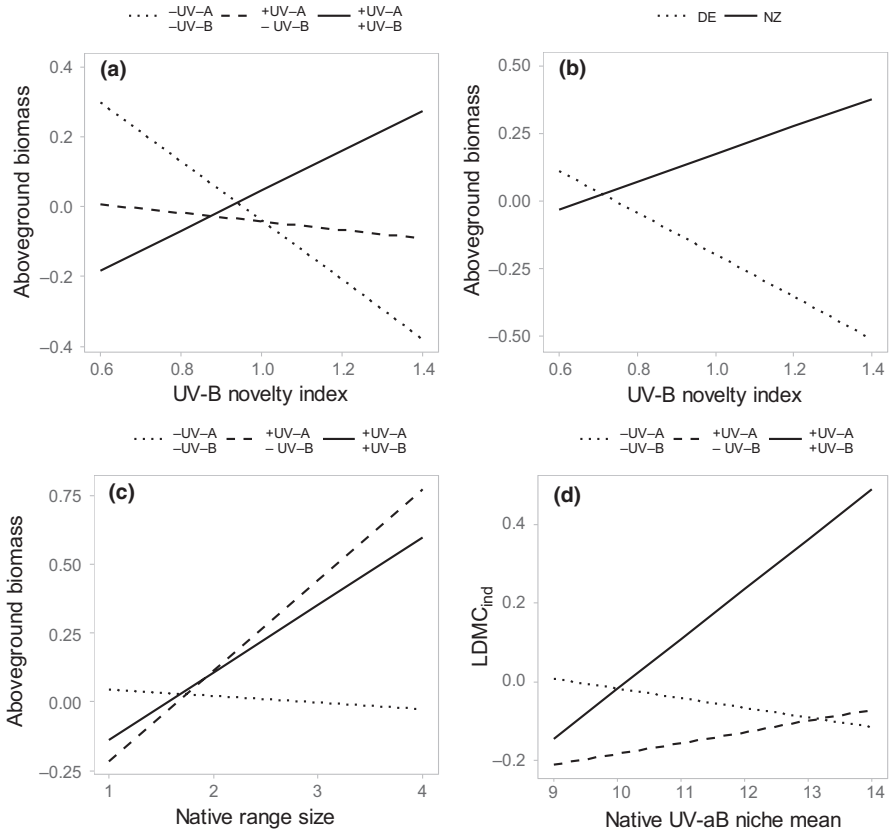

FIGURE 2 (a-d): Test for climatic preadaptation: Effects of the "UV-B novelty index" on aboveground biomass (a) across the different UV treatments and (b) across the experimental sites Germany (DE) and New Zealand (NZ); effects of (c) the native range size on aboveground biomass and (d) the native UV-B niche mean [kJ m^{-2} day^{-1}] on leaf dry matter content ($LDMC_{ind}$) across the different UV treatments. Predicted values of z-scores from the respective full statistical model identified by model selection are shown for experimentally determined dependent variables

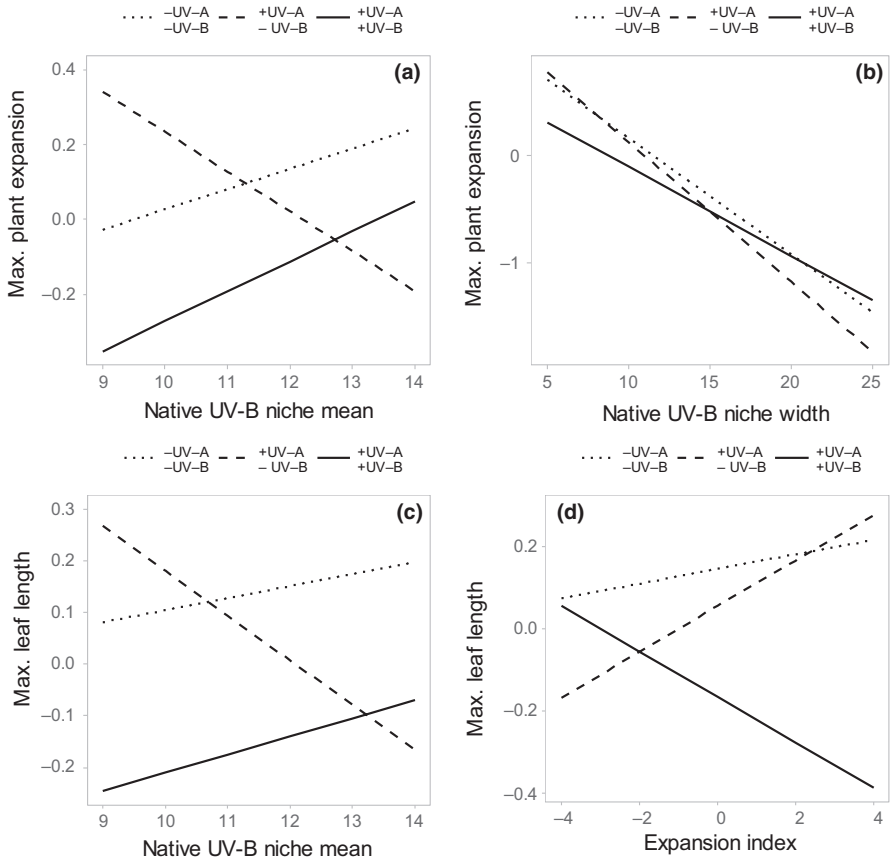

FIGURE 3 (a-d): Test for climatic preadaptation: Effects of (a) the native UV-B niche mean on maximum [kJ m^{-2} day^{-1}] horizontal plant expansion, (b) the native UV-B niche width [kJ m^{-2} day^{-1}] on maximum horizontal plant expansion, (c) the native UV-B niche mean [kJ m^{-2} day^{-1}] on maximum leaf length, and (d) the "expansion index" on maximum leaf length across the different UV treatments. Predicted values of z-scores from the respective full statistical model identified by model selection are shown for experimentally determined dependent variables

lower SLA and higher LDMC (Yang et al., 2019). In our study, this classical trade-off of SLA and LDMC in the leaf economics spectrum was confirmed under UV exclusion at both experimental sites (Poorter & Garnier, 1999). However, only in the presence of UV-B radiation, we observed a positive relationship of specific leaf $area_{spec}$ with leaf dry matter $content_{ind}$, thereby indicating that an increase of leaf tissue density took place to a greater extent in large-SLA_{spec} leaves when exposed to UV-B (Shipley & Vu, 2002). This effect underlines the widespread occurrence of leaf morphological plasticity in foliar adaptation to high irradiance environments (Niinemets, Kull, & Tenhunen, 1998), and in particular for plant species with a lower SLA. As SLA is a compound trait that is not only responding to the underlying LDMC but is also affected by the light-dependent trait leaf thickness, we infer that the most responsive species under UV-B radiation suffer from photoinhibition due to insufficient leaf thickness and/or leaf tissue density (Hodgson et al., 2011).

Regarding the study aim to identify suitable traits in the context of appropriate preadaptation to high-UV-B environments, especially significant interaction effects of the tested "preadaptation indicators" with "UV treatment" and "experimental site" are of high importance. Interaction effects with "UV treatments" directly point at the importance of respective "preadaptation indicators" for plant performance in particular UV-B environments as applied by the different UV treatments within both experimental sites. Additional corresponding interaction effects of the particular "preadaptation indicator" with "experimental site" can be ascribed to differences in overall UV-B intensities between Germany and New Zealand, but may also indicate other differences in environmental conditions. Nevertheless, corresponding interaction effects of preadaptation indicators with both experimental predictors representing different UV-B environments are most interesting as they might support the effect of UV filter treatments at a larger scale.

The observed effects of persistent leaves and high specific leaf $area_{spec}$ across the UV treatments were confirmed by the experimental site comparison, as both recur in the "high-UV-B" environment New Zealand. This consistency additionally underpins the importance of the UV-B intensity differences between the experimental sites.

Overall, there was only little evidence of a sufficient preadaptation of our study species to UV-B by functional (leaf) traits. Instead, there rather might be indirect effects of functional leaf traits in terms of facilitating cross-resistance effects in association with other environmental stresses, for example drought or herbivory (Kergunteuil, Descombes, Glauser, Pellissier, & Rasmann, 2018). Herbaceous species of grasslands might be specifically adapted to low water availability or water loss from high transpiration, for example, by smaller leaves with predicted higher UV-B resistance (Bandurska, Niedziela, & Chadzinikolau, 2013). Moreover, leaves equipped with secondary metabolites, for example phenolics, are at the same time resistant to herbivory and photodamage by high-UV-B intensities (Kuhlmann & Müller, 2011).

4.3 | Evidence for climatic preadaptation to high-UV-B environments

Within the tested group of biogeographic characteristics, we can distinguish between traits that may predominantly convey an indirect preadaptation to a broad range of climatic conditions, such as range size and "expansion index," and traits that may be rather directly associated to already experienced UV-B intensities, such as native range UV-B niche characteristics. In the present study, the latter group of traits appeared to be of greater importance in the context of UV-B preadaptation, as one would expect (Thuiller et al., 2005).

Species with a large native range and experiencing high maximum UV-B intensities in their native ranges produced more biomass in the presence of UV radiation than species with a different native range history (Pyšek et al., 2009). In principle, both indirect and direct preadaptation appeared to prevail in our study species. Against our expectations, species with a wider native UV-B niche did not display a general advantage although it may be likely to indicate higher levels of experienced UV-B intensities in the native range. This effect was probably not observed because using one population per species only can hardly serve as a reference for the entire range of UV-B intensities experienced in the native range. We have to assume that each population in our experiment is rather adapted to the local UV-B conditions of the particular population origin. Interestingly, we found a positive relationship between "UV-B novelty index" and aboveground biomass in UV-B environments, that is, relatively higher exotic than native annual mean UV-B coincided with increased productivity. This unexpected result rather opposed our hypothesis of species being preadapted by native range UV-B intensities and might indicate higher importance of cross-resistance mechanisms in herbaceous species compared to prior UV-B experience. An alternative explanation might be the unsuitability of the preadaptation indicator "UV-B novelty index," as it is based on the annual mean UV-B intensities of the native and exotic range, that are likely to be not as important for physiological processes in plants as summer mean UV-B intensities or maximum UV-B intensities during the year (see Hideg, Jansen, & Strid, 2013).

The higher "expansion index" (size of exotic range related to native range size) of species affected maximum leaf length only, above all also in negative direction in presence of UV-B, and, therefore, appeared not to be of advantage in high-UV-B environments. On the one hand, this effect might confirm the assumption of higher phenotypic plasticity of alien species with a large exotic range in response to UV-B and the necessity of that particular ability to successfully colonize novel habitats (Oplaat & Verhoeven, 2015; Ruprecht, Fenesi, & Nijs, 2014; Turner, Fréville, & Rieseberg, 2015). On the other hand, a higher "expansion index" could also be the result of a very confined native range that might display a disadvantage in the context of climatic preadaptation to high-UV-B radiation intensity (Pyšek et al., 2009). $LDMC_{ind}$ was the only functional plant response that showed an interaction effect of UV treatments with the tested biogeographic characteristics. The higher the mean UV-B intensities in their native range, the higher was the $LDMC_{ind}$ under UV-B radiation exposure. As LDMC is known for its ability to respond plastically and its protective effect against high-energy radiation, one could expect a more pronounced response of preadapted species as observed in the experiment (Hock et al., 2019; Robson et al., 2015).

We found further indication for the mitigating effect of UV-A radiation on the growth variables maximum horizontal plant expansion and maximum leaf length. In presence of UV-A radiation only, existing positive relationships between maximum horizontal plant expansion and maximum leaf length with native range mean UV-B intensity were abrogated or even reversed. In consequence, plant species without direct UV-B preadaptation by higher native range mean UV-B intensity profited from UV-A exposure, that is known to stimulate plant growth (Escobar-Bravo et al., 2017; Štroch et al., 2015; Verdaguer et al., 2017). Potentially well-preadapted species, on the other hand, appeared to be disadvantaged by UV-A radiation for any reason. One explanation may be found in well-developed shielding abilities of preadapted species that might also block UV-A wavelength and their facilitative effects on plant growth.

5 | CONCLUSIONS

With regard to UV-B preadaptation, we found strong evidence for the importance of biogeographic characteristics, whereas functional preadaptation by plant traits played a moderate role (see also Chen, Peng, & Yang, 2015). Especially, biogeographic characteristics with a direct link to the native range UV-B niche were crucial for plant responses to UV-B. Our results call for explicitly considering the native UV-B niche as a proxy for species' UV-B tolerance when making species distribution predictions in high-UV environments. Furthermore, our findings support the assumption that high phenotypic plasticity across differing UV-B environments is an important factor that might also affect the performance of alien species. We conclude that explicitly considering UV-B radiation in native and exotic ranges is important for improving the understanding of the factors modulating invasion success and should also be taken into account in models of biological invasions.

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DATA AVAILABILITY STATEMENT

Plant trait data (TRY) and native/exotic distribution data (GBIF, GloNAF) used in this study were obtained from third parties, either through open access digital repositories or through formal data sharing agreements. The authors do not have permission to distribute these data without explicit consent from its contributors. The experimental data of the two conducted common garden experiments and the used statistical models will be made available via the Dryad Digital Repository https://doi.org/10.5061/dryad.b5mkkwh9g.

ORCID

Maria Hock https://orcid.org/0000-0001-8401-7309
Rainer Hofmann https://orcid.org/0000-0002-1804-2319
Franz Essl https://orcid.org/0000-0001-8253-2112
Petr Pyšek https://orcid.org/0000-0001-8500-442X
Helge Bruelheide https://orcid.org/0000-0003-3135-0356
Alexandra Erfmeier https://orcid.org/0000-0002-1002-9216

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BIOSKETCH

Maria Hock is currently a PhD candidate at Kiel University, and her main research focus is on adaptability of invasive grassland species to high levels of UV-B radiation and the impact of UV-B radiation as a potentially selective environmental filter during plant invasions in New Zealand.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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